THE INNERVATION OF THE STOMACH AND RECTUM AND THE ACTION OF ADRENALINE IN ELASMOBRANCH FISHES

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A study of the literature concerning the innervation of the stomach and intestine in mammals reveals much confusion and contradiction. The orthodox differentiation into sympathetic and parasympathetic with antagonistic actions has many exceptions. Thus Langley (1898) found inhibitory fibers to the stomach in the vagus of the rabbit, Morat (1893) found excitatory fibers to the stomach and intestine in the splanchnic of the dog, and Carlson, Boyd and Pearcy (1922) have found that both the splanchnics and the vagi of the cat carry both kinds of fibers to the stomach. On the basis of effects produced by adrenaline, Smith (1918) assumed the splanchnics to be inhibitory for the stomach in man and in the cat, but only for certain parts of the stomach in the guinea pig, rabbit and dog, while being motor for other parts. Tashiro (1920), however, using adrenaline on surviving cat intestine, came to the conclusion that there are motor fibers to the circular muscle in the sympathetic nerves as well as inhibitory fibers to both the circular and the longitudinal layers. McCrea, McSwiney and Stopford (1925) found that in dogs, cats and rabbits the primary effect of stimulation of the peripheral cut end of the vagus on the stomach may be inhibition or augmentation, depending upon the intragastric pressure, but that the final effect is motor. Brown, McSwiney and Wadge (1930) found that the effect of sympathetic stimulation depends on the type of stimulation. A low frequency contracted the body of the stomach in the cat, whereas ordinary tetanizing current inhibited. All rates inhibited the antrum, and adrenaline caused an inhibition of both parts. In a review Van Campenhout (1930) says, "We believe the actual distinction of sympathetic, parasympathetic and local innervations to be erroneous owing to ignorance of the real constitution of the visceral autonomic nervous system." A similar view was expressed by Langfeldt (1929), who concluded that there is no absolute antagonism between the sympathetic and parasympathetic and that our information concerning the peripheral termination of both systems is incomplete.

The literature concerning the visceral innervation in the lower vertebrates shows no more conformity to the orthodox view than does that in mammals. Goltz (1872) showed that the splanchnic nerves are motor for the stomach in the frog, and this has been confirmed by Dixon (1902), Müller and Liljestrand (1918) and Itagaki (1930). Dixon (1902) found the vagus in the frog to have either an inhibitory or a motor effect on the stomach. For reptiles there is not enough evidence to make a comparison, either anatomical or physiological, although Thorell (1927) by the use of adrenaline considered the sympathetic to be inhibitory to all parts of the turtle's stomach except the cardiac portion. In birds Nolf (1925) has reported that the vagus is motor to the crop, and either motor or inhibitory to the gizzard and small intestine; and the coeliac nerves are either motor or inhibitory to the gizzard and duodenum.

In elasmobranch fishes the autonomic nervous system appears not to be well developed (Müller and Liljestrand, 1918). Bottazzi (1902) found both the vagus and the anterior splanchnic nerves in *Scyllium canicula* to be motor for the stomach. He was unable to demonstrate any inhibitory effect of either. Stimulation of the cord in the region from the forty-fifth to forty-eighth spinal nerves gave motor activity of the rectum. Müller and Liljestrand (1918) confirmed Botazzi (1902) in part, using *Squalus acanthias* and various species of *Raia*, but believed an inhibitory effect of the vagus on the stomach to be more marked than the motor effect. They never obtained evidence of inhibition from the anterior splanchnics. Stimulation of the middle and posterior splanchnic nerves was without effect on the spiral valve and rectum.

In view of other peculiarities of the autonomic nervous system in elasmobranchs, namely, the lack of accelerator nerves to the heart (Bottazzi, 1902; Müller and Liljestrand, 1918; Lutz, 1930*a*) and the inhibitory action of adrenaline on the heart (Macdonald, 1925; Lutz, 1930*b*), the present writer believed that it might prove useful to compare the effects of adrenaline and extract of chromaphil tissue on parts of the gut with the effects of electrical stimulation of the extrinsic nerves to the same parts.

Material and Method

The elasmobranchs used were *Squalus acanthias*, *Raia erinacea* and *R. diaphanes*. For anatomical reasons only *S. acanthias* was used when nerves were stimulated. Segments of the stomach, spiral valve, and rectum one half to one inch long were suspended in 50 cc. of a physiological solution described by Lutz (1930*b*), and tracings obtained. Some pieces were hung so that the circular muscles would activate the lever, others were suspended so that the longitudinal layer would be most effective. Adrenalin chloride (Parke, Davis & Co.) and chromaphil tissue extracted in distilled water were added to the bath by means of a pipette. Control tests, in which similar amounts of distilled water and extracts of liver and spleen were added to the bath, showed that the method was satisfactory. An extract of the anterior chromaphil bodies was made in one cc. of distilled water immediately on removal of the tissue, and used at once. In a few cases, in which *R. stabuliforis* served as a source of chromaphil tissue, only one "axillary heart" was used to one cc. of distilled water,

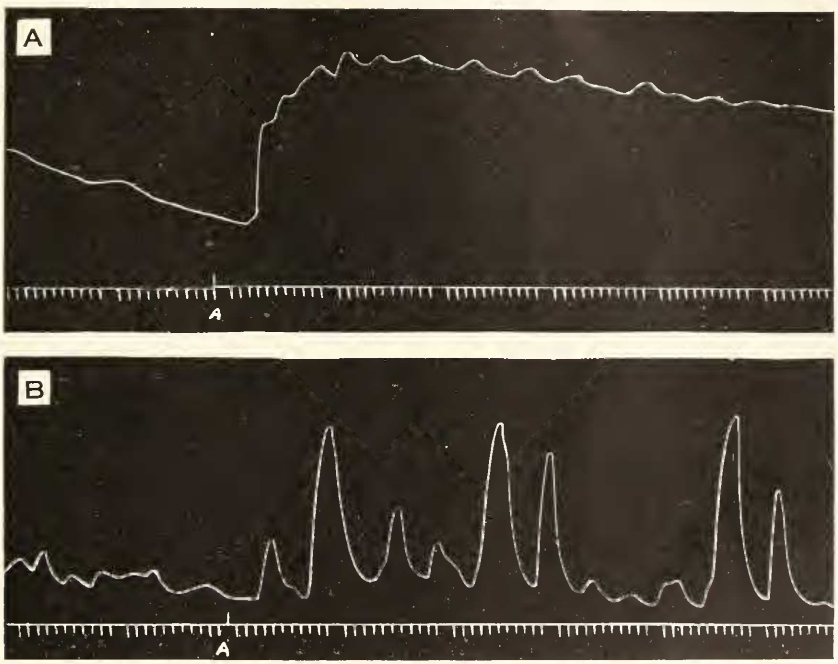

FIG. 1. Effect of adrenalin chloride, 1 in 50,000, on the pyloric portion of the stomach. Time in 5 second intervals. *A*, *Raia erinacea.* Typical effect on tonus. *B*, *R. diaphanes.* Effect mainly on motility.

but in the case of the smaller species of *Raia* both anterior chromaphil bodies were used and sometimes, in addition, some of the accessory bodies.

In the experiments in which the extrinsic nerves were stimulated the entire central nervous system was pithed. The left vagus was exposed through the anterior cardinal sinus. The first sympathetic ganglion (gastric) and the anterior splanchnic nerves were exposed through the posterior cardinal sinus, or the latter were sometimes stimulated along the course of the coeliac artery. The posterior splanchnic nerves (rectal) were stimulated along the posterior mesen-

FIG. 2. Effect of adrenalin chloride, 1 in 50,000, on the rectum of *Squalus acanthias*. Time in 5 second intervals. At *M*, 2 cc. of the bath fluid squirted on the preparation. Adrenalin chloride added at *A*.

teric artery or in the mesentery supporting the rectal gland. Records of the movement of the gut were obtained by means of a small hook and a light lever. The nerves were stimulated with faradic current by means of platinum electrodes leading from an inductorium (Harvard Apparatus Co.) with the secondary coil set at 8 cm. and one 2.5 volt dry cell in the primary circuit.

RESULTS

Adrenalin chloride added to the bath fluid to make one in 50,000 caused a rise in tone and sometimes augmentation of rate and height of the movements of the pylorus and other parts of the stomach in twenty-five preparations and had no effect in three cases (Fig. 1).

In some inactive preparations motility was initiated by a similar dose. A distilled water extract of chromaphil tissue taken from the skate gave the same effect as adrenalin chloride on the pylorus and stomach of both the skate and the dogfish (Fig. 3). Extracts of liver and spleen, agitation of the bath fluid, or the addition of distilled water gave no response.

On twelve preparations of the posterior end of the spiral valve and the rectum, adrenalin chloride, one in 50,000 caused a marked fall in tone and an inhibition of motility (Fig. 2). In no case was

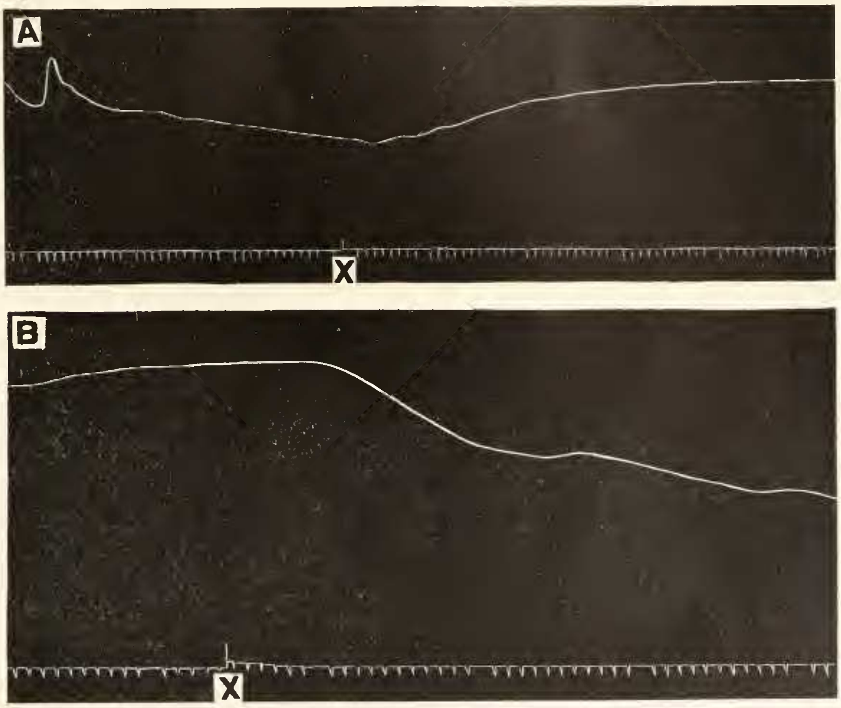

FIG. 3. Effect of extract of chromaphil tissue. Time in 5 second intervals. *A*, *Squalus acanthias*, pyloric portion of the stomach. *X*, extract of the axillary bodies from one side of *Raia stabuliforis*. *B*, *R. erinacea*, rectum. *X*, extract of the axillary bodies of the same specimen.

there activation or failure of response. Extract of chromaphil tissue also caused inhibition (Fig. 3). Extract of liver gave no response.

In thirteen specimens of *S. acanthias* faradic stimulation of the first sympathetic ganglion (gastric) or the anterior splanchnic nerves caused extensive contractions of the stomach beginning in the pyloric region. The latent period varied from two to five seconds (Fig. 4, *A*).

In seven fishes faradic stimulation of the peripheral end of the cut vagus at the anterior cardinal sinus caused moderate contractions of the pylorus and adjacent region. The latent period was about five seconds. In one case no response was obtained. The response from the vagus was never obtained longer than forty minutes after the

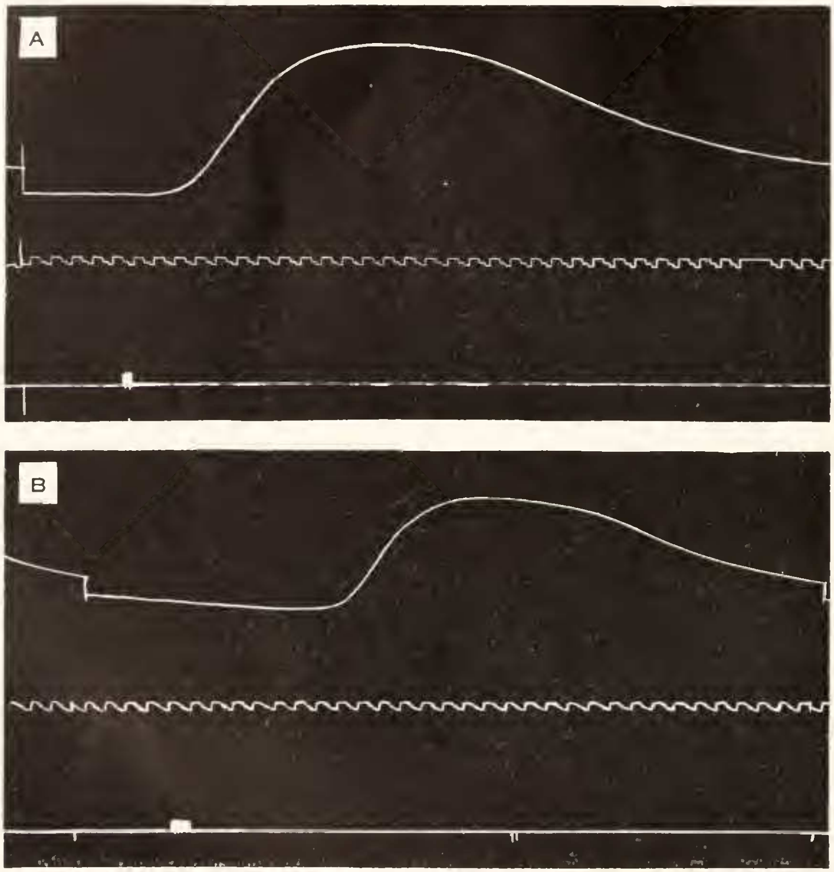

FIG. 4. Effect of faradic stimulation. Time in seconds. *A*, *Squalus acanthias*. Contraction of the pyloric portion of the stomach on stimulating the first sympathetic ganglion (gastric) for one half second. Latent period, 2.5 seconds. *B*, *S. acanthias*. Contraction of the rectum on stimulating the posterior splanchnic nerves for one second. Latent period, 8 seconds.

opening of the cardinal sinuses, whereas the sympathetic response was obtained after three hours.

In four fishes the posterior splanchnic nerves were stimulated and in each case a vigorous contraction of the rectum and the adjacent part of the spiral valve was repeatedly obtained (Fig. 4, *B*). The response had a latent period of eight to ten seconds, and in one specimen was active after three hours without the circulation.

Discussion

The motor effect of electrical stimulation of the sympathetic and of adrenaline on the stomach of the elasmobranch is another exception to the view that in general the sympathetic is inhibitory to the gut and the vagus motor. In this case the effect of adrenaline is sympathico-mimetic. If the posterior splanchnic nerves, stimulation of which activates the rectum, are sympathetic, as Müller and Liljestrand (1918) describe them to be, then the inhibitory action of adrenaline on this part of the intestine is also an exception. Brown, McSwiney and Wadge (1930) found that adrenaline did not reproduce the effects of sympathetic stimulation of the stomach in the cat and in the dog, inhibition being the invariable result.

The results reported here confirm Bottazzi (1902) working on *Scyllium*, and Müller and Liljestrand (1918) working on *Squalus* and *Raia* insofar as the effect on the stomach of electrical stimulation of the anterior splanchnic nerves is concerned. However, since a marked contraction of the rectum resulted from stimulation of the posterior splanchnic nerves, and no evidence of inhibition of the stomach through stimulation of the vagus was obtained, these results are to that extent at variance with those of Müller and Liljestrand.

While there may be a valid reason for perpetuating the morphological division of the autonomic nervous system into cranial, thoracolumbar and sacral parts, there is sufficient evidence to indicate that a general physiological distinction should not be made so far as control of the alimentary tract is concerned.

Summary

1. Adrenalin chloride and extract of the chromaphil bodies caused a rise in tone and sometimes an increase in motility of all parts of the stomach of *Squalus acanthias*, *Raia erinacea* and *R. diaphanes*.

2. Faradic stimulation of the first sympathetic ganglion (gastric) and the anterior splanchnic nerves caused extensive contractions of the stomach beginning at the pylorus in *Squalus acanthias*. Similar stimulation of the vagus caused moderate activity in the region of the pylorus.

3. Adrenalin chloride and extract of chromaphil bodies caused a marked decrease in tone and inhibition of motility of the posterior end of the spiral valve and the rectum in all three elasmobranchs.

4. Faradic stimulation of the posterior splanchnic nerves caused a vigorous contraction of the rectum and adjacent part of the spiral valve in *Squalus acanthias*.

5. The data presented here and the evidence from the literature indicate that a general physiological distinction between the sympathetic and the parasympathetic divisions of the autonomic nervous system should not be made.

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